Desert Truffles

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Abstract

Desert truffles are nutritious hypogeous mushrooms exhibiting unusual biological features. They are mycorrhizal and may form either or both of two main types of associations, ecto- or endomycorrhizae. These fungi inhabit sandy soils and require little water. Desert truffles have been collected from the wild by desert dwellers from early stages of civilization. With the exception of some Tuberaceae family members, truffle members of the order Pezizales have been rather neglected by science. Efforts at their cultivation are being undertaken, and this paper will review much of what is currently known of these mysterious and fascinating desert fungi.

Introduction

Desert truffles, though less appreciated culinarily than the European forest ones, are nonetheless true truffles in the sense that they are hypogeous (underground) ascomycete fungi, as opposed to hypogeous basidiomycete fungi, termed false truffles.

The desert truffles were traditionally grouped into the Terfeziaceae family of fungi, within the order Tuberales. However, molecular phylogenetic studies of sequestrate fungi have repeatedly demonstrated that the morphology of hypogeous fungi can be misleading due to reduction in macromorphological characters needed for distinguishing their related epigeous taxa. Thus O'Donnell et al. (1997) and Hansen et al. (2001) demonstrated that certain hypogeous fungi show greater affinity to epigeous members of the Pezizales than to other hypogeous species. It seems that at least 15 independent incidents of epigeous fungi evolving the below-ground fruiting habit to become truffles occurred within the Pezizales (Hansen, 2006). The best known and appreciated genera *Terfezia* and *Tirmania* were shown to belong to the Pezizaceae rather than to the distinctly hypogeous Terfeziaceae family, which has been abolished (Norman and Egger, 1999; Percudani et al., 1999). In fact, hypogeous ascomycete fungi (truffles) are now distributed among six Pezizalean families: Glaziellaceae, Discinaceae-Morchellaceae, Helvellaceae, Tuberaceae, Pezizaceae, and Pyronemataceae, comprising 38 genera (Hansen, 2006). The family Tuberaceae, which includes the most highly prized (and priced) forest truffles is the single family containing only underground species (Hansen, 2006).

We will concentrate on hypogeous members of the Pezizaceae, which in its turn underwent some reshuffling of members within the family. Thus, the genus *Choiromyces* was transferred from the Pezizaceae to the Tuberaceae (O'Donnell et al., 1997; Percudani et al., 1999), although one *Choiromyces* species, *C. echinulatus*, was excised from this genus and restored to the Pezizaceae under a new name, *Eremiomyces echinulatus* (Ferdman et al., 2005). Similarly, two species were removed from the *Terfezia* genus: *Terfezia terfezioides*, reinstated as *Mattirolomyces terfezioides* (Percudani et al., 1999; Diez et al. 2002), and *Terfezia pfeilii*, renamed *Kalaharituber pfeilii* (Ferdman et al., 2005). Cryptic species (truffles that are morphologically identical but molecularly rather distinct and distant from each other) are coming to light, including a group of three discovered within the *T. boudieri* desert truffle complex (Ferdman, 2006). The Pezizaceae includes (among others) the following hypogeous genera: *Eremiomyces, Hydnotryopsis, Kalaharituber, Mattirolomyces, Pachyphloeus, Peziza, Ruhlandiella, Stephensia, Terfezia,* and *Tirmania* (Laessøe and Hansen, 2007). Of these *Terfezia* is the held in the highest regard for eating; *Kalaharituber*, *Tirmania,* and *Mattirolomyces* follow.

With the exception of some Tuberaceae family members, truffle members of the order Pezizales have been rather neglected by science. Our knowledge on the physiology, biochemistry, and plant-fungus relations of the hypogeous members of Pezizaceae is therefore fragmentary.

All truffles known so far, desert truffles included, are mycorrhizal. The known and edible Mediterranean desert truffle genera usually occupy the same habitat and often share the same host plants. Fruit bodies range in weight from about 30 to 300 g per truffle, that of the main body being about 100 g, and are subglobose and, at times, multi-lobed (Figures 1 and 2).

The recent interest in desert truffles, especially of the genera *Terfezia* and *Kalaharituber,* as potential candidates for cultivation (Honrubia et al., 2002; Kagan-Zur et al., 1999) will, it is hoped, motivate more investigation of these genera; it has already generated several (albeit limited) biochemical studies of enzy-

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Figure 1. Terfezia, *photographed by Elinoar Shavit.*

matic activities in one species of desert truffle (Perez-Gilabert et al., 2001a; 2001b; 2004; 2005).

Nutritional Value

Less than exhaustive studies of the composition and nutritional value of desert truffles have been carried out in those countries where they are known and appreciated. It appears that the dry matter (about 20% by weight) consists of 20–27% protein, some 85% of which is digestible by humans (although it was recently concluded that the protein quality of four studied species is low); 3–7.5% fat, including unsaturated as well as saturated fatty acids; 7–13% crude fiber; close to 60% carbohydrates; and appreciable amounts (2–5%) of ascorbic acid (Ackerman et al., 1975; Al-Delaimy, 1977; Al-Shabibi et al., 1982; Sawaya et al., 1985; Bokhari et al., 1989; Saqri, 1989; Bokhari and Parvez, 1993; Dabbour and Takruri, 2002; Murcia et al. 2003). High levels of potassium and phosphate and fair amounts of iron have been reported (Saqri, 1989). Some studies of suitable methods for their preservation have been undertaken (Murcia et al., 2003).

No known toxic compound has been detected (Ahmed-Ashour et al., 1981). On the contrary, it was shown that the Saudi desert lore claiming that truffle extract is effective against the eye disease trachoma has a scientific basis (Al-Marzooky, 1981), and evidence of a rather broad antibiotic activity of truffle extracts has emerged (Janakat et al., 2004; 2005),

Distribution

Underground members of the Pezizaceae are well distributed around the globe. They are found in arid and semiarid zones of the Mediterranean basin, Iraq and Kuwait, the Sahara and Saudi Arabia (see Trappe, 1990), Hungary (Kiraly and Bratek, 1992), Yugoslavia (Lawrynowicz at al., 1997), China (Zhang, 1992), the Kalahari desert (Marasas and Trappe, 1973; Trappe, 1990; Ferdman et al., 2005), Australia (Francis and Bougher, 2002; Lebel and Castellano, 1999), and North America (Trappe and Castellano, 1991; Izzo et al., 2005; and see also Laessøe and Hansen, 2007). These hypogeous fungi are popularly termed "desert truffles" to distinguish them from the highly esteemed Tuberaceae truffles of the genus *Tuber,* however, not all are found uniquely in deserts (e.g. *Mattirolomyces*, Laessøe and Hansen, 2007, and others).

In certain habitats, such as Saudi Arabia, Kuwait, parts of the Magreb, and the Kalahari, fruit bodies of desert truffles have been collected and appreciated as a food or delicacy from ancient times to this day (Trappe, 1990). They are also appreciated by Aborigines in the Australian desert (Lepp and Fagg, 2003). In other habitats, such as China, they were little known before modern times (Milius, 2008). Their appreciation is now taking off.

Growth Habits

Symbionts

Terfezia spp. and *Tirmania* spp. form mycorrhizae mainly on roots of members of the Cistaceae family, including different species of the genus *Helianthemum* (Awameh, 1981; Dexheimer et al., 1985; Morte et al., 1994; Roth-Bejerano et al., 1990), but have other

Figure 2. Tirmania, *photographed by the late Mr. Y. De-Malach, Revivim.*

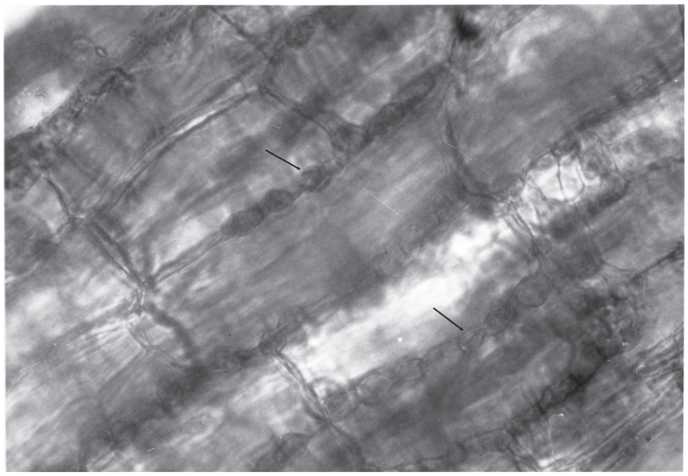

Figure 3. Ectomycorrhizal associations between Terfezia boudieri *and* Helianthemum sessiliflorum. *Fungal cells (arrows) (bead-like cells) surround plant root cells.*

symbionts as well. Both perennial (Roth-Bejerano et al., 1990) and annual (Awameh and Alsheikh, 1978) plants of the above family may support *Terfezia* and *Tirmania* mycorrhizae, though possibly, with some specificity as to the truffle species. In southern Africa, where no members of the Cistaceae grow (Riley, 1963; Heywood, 1993), we were recently able to show that watermelon (*Citrullus vulgaris*), a domesticated plant, functions as a plant symbiont for *Kalaharituber pfeilii* (Kagan-Zur et al., 1999). Watermelon is presumably not the original (and certainly not the sole) symbiont, as this truffle also occurs in areas where watermelons do not. Certain *Acacia* species are the natural plant hosts (Kagan-Zur and Roth-Bejerano, unpublished). Thus, the Kalahari truffles can expand their host range opportunistically. Recently it was shown that at least one *Tefezia* species can also expand its host range and infect oak seedlings when the latter grow near *Helianthemum* (Dickie et al., 2004). Note that while *Terfezia* and *Tirmania* preferentially form mycorrhizae with annuals and bushes, *K. pfeilii* preferentially forms mycorrhizae with trees. However, so does *Mattirolomyces terfezioides*, which enters into mycorrhizal symbioses with tree roots (*Robinia pseudoacacia*).

Types of Mycorrhizal Symbioses

As a rule of thumb, all members of the same mycorrhizal fungal family will produce the same type of association in the wild; i.e. either ectomycorrhizal (fungal cells do not penetrate plant cells and form Hartig net [Fig. 3] and club like root tips which are covered by a fungal sheath, called a mantle) or endomycorrhizal (fungal cells proliferate within plant cells forming tree like structures called arbuscules). The desert truffles are exceptional in this respect. Different species have been observed to form different mycorrhizal types with the same plant species. *Terfezia leptoderma* (Chevalier et al., 1984; Dexheimer et al., 1985) and *Terfezia arenaria* (*leonis*) (Roth-Bejerano et al., 1990; and unpublished data) produce a Hartig net without mantle—essentially an underdeveloped ectomycorrhiza in roots of different Cistaceae species. *Terfezia boudieri* (Awameh, 1981; Alsheikh, 1984), *T. claveryi* (Alsheikh, 1984; Dexheimer et al., 1985), *Tirmania nivea* and *Tir. pinoyi* (Alsheikh, 1984), and *Kalaharituber pfeili* Kagan-Zur et al., 1999) were reported to form endomycorrhizae lacking Hartig net and mantle but displaying undifferentiated intracellular hyphae (Figure 4).

Figure 4. Endomycorrhizal associations between Kalaharituber pfeilii *and watermelon roots. Fungal hyphae (arrows) entangle within cells.*

Thus the desert truffle family could be regarded as transitional between true ectomycorrhizal and true endomycorrhizal. Furthermore, the boundaries between ecto- and endomycorrhizal types are somewhat fluid, and the character of the mycorrhiza formed is often determined by external conditions. Fortas and Chevalier (1992) studied *Helianthemum guttatum* colonized by either *Terfezia arenaria, T. claveryi,* or *Tirmania pinoyi* and found a shift from ectomycorrhizae at high phosphate (P) concentration to endomycorrhizae at low concentration. Moreover, Gutierrez et al. (2003), working with *Helianthemum almeriense* colonized by *Terfezia claveryi* and *Picoa lefebvrei*, encountered only endomycorrhizae under field conditions, only ectomycorrhizae *in vitro* (with a mantle, the only report of a mantle in a *Terfezia* mycorrhiza), and mostly ectomycorrhizae lacking a mantle in pots under greenhouse conditions.

Using an *in vitro* system in which several transformed root clones of *Cistus incanus* (Wenkart et al., 2001) were paired with different isolates of *Terfezia boudieri*, Zaretsky et al. (2006) concluded that the type of mycorrhiza obtained, endo- or ectomycorrhizal, depends on the following:

a. Genetic background of both fungal isolate and plant clone
b. Phosphate concentration in the growth medium
c. Plant sensitivity to auxin (a plant hormone)
d. Level of auxin secretion by the fungal isolate

Soil and Climatic Parameters

Most of the species develop in high pH calcareous soils (Fortas and Chevalier, 1992; Giovannetti et al., 1994), but some are found in soils with below neutral pH values (Kiraly and Bratek, 1992; Taylor et al., 1995). Most occur in rather sandy soils (Table 1). In several countries there are legends connecting truffle appearance to thunderstorms early in the rainy season. The Bedouin of the Israeli Negev tell the same story as truffle hunters in Morocco (Kagan-Zur, personal observations) and Syria (MacFarquhar, 2004). The only verified fact is that desert truffle yields in the wild are highly dependent on rainfall and rain distribution during the rainy season, though as little as 200–250 mm per season may bring forth a good yield.

Table 1. Some characteristics of the topsoil of Terfezia productive fields (note range of variation).

	Terfezia spp.	***Kalaharituber pfeilii***
pH	7.9–8.5	5.5–6.5
CaCO3 (total) %	4–54	0.5–3.1
Soil composition		
Sand %	80–90	94–97
Silt %	1–8	1–4
Clay %	4–9	2–5

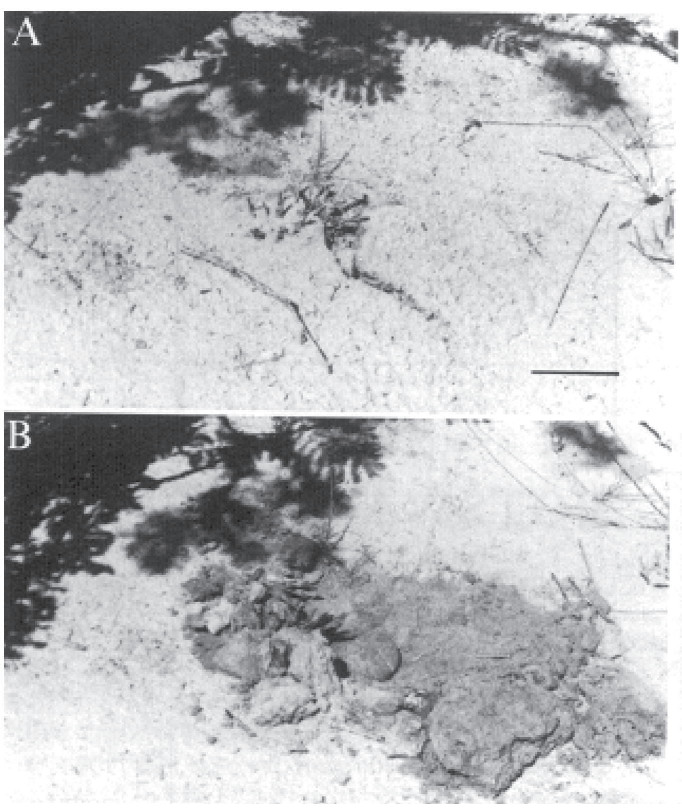

Figure 5. Truffle location. A. Cracked and swollen soil surface. B. The uncovered truffles. Reprinted from Taylor et al. 1995, with kind permission of Mycological Research.


Figure 6. A truffle with its "stalk." Photographed by the late Dr. David Mills.

Locating Fruit Bodies

One does not have to rely on trained dogs or pigs to collect desert truffles, as is the case with European forest truffles. Fruit bodies develop close to the soil surface; and as they swell, they lift up the soil to form cracked little mounds recognizable to the trained eye (Awameh and Alsheikh, 1978; Taylor et al., 1995; Fig. 5). The fruit bodies are carried up on a "stalk" (Fig. 6) composed of entangled hyphae and sand particles. Some lack parenchymatous tissue (Taylor et al., 1995), while others have such tissue (Kagan-Zur & Roth Bejerano, unpublished observation). The bottom of the stalk, which is between 2 and 10 cm in length, is connected to rhizomorphs (Taylor et al., 1995) and to hyphae emanating from adjacent roots. The rhizomorphs lead from colonized roots to the fruit body, which may lie as much as 40 cm away.

Cultivation

Cultivation of desert truffles is not trivial, and for decades was not a priority, as desert truffles are considered inferior to the much-praised forest truffles. As mentioned above, desert truffles are becoming more desirable of late, and some research is now dedicated to their cultivation. However, the only report of successful man-made desert truffle plantations to date comes from Spain, where *T. claveryi* was cultivated in symbiosis with *Helianthemum almeriense* (Honrubia et al., 2002; Hall et al. 2007).

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More False Truffles. Photos by John Plischke III.

Rhizopogon cinerascens.

Rhizopogon ochraceoialiens.

Rhizopogon subaredatus.